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A series of culture experiments with the Uredinales was begun by the writer in 1899, and continued under the auspices of the Indiana Agricultural Experiment Station without interruption until 1917, making nineteen consecutive years in which this method of research was consistently pursued. The results of the work were embodied in fifteen reports, printed in the Botanical Gazette, Journal of Mycology, and Mycologia. It is now proposed very briefly to review the work, in order to set forth some of the objects accomplished, and especially to point out the more important of the changing conceptions of the problems forming the ground plan on which the work was projected.

The cultures were not undertaken as part of a distinct thesis or circumscribed problem. They were rather the aids in a general taxonomic study of American rusts, which was directed toward supplying a technical description as complete as possible for every species of Uredinales in North America recorded in literature or known to the writer. This ambitious undertaking was definitely begun sometime in the nineties at the invitation of the editors of the North American Flora.

Beginning with my first taxonomic work on the rusts in 1882 it had seemed to me highly desirable for the purposes of a full technical description of species, that every part of these microscopic plants, capable of supplying diagnostic characters, should be uniformly considered, quite as much as are the stems, leaves, inflorescence, flowers, and fruit of higher plants, and that every means should be taken to arrive at a clear understanding of the identity and relationship of the various forms and species. No effort should be spared, it was believed, to make the name applied to any form embrace also the transformations and variations

[1] Contribution from the Botanical Department of Purdue University Agricultural Experiment Station.

which that form undergoes in passing through its whole life cycle. Many rusts are commonly collected in only one or two stages of their development, or the several stages are taken as independent objects, and to grow such rusts so as to keep them under direct observation and be able to note the succession of stages seemed highly desirable, and especially so for the heteroecious species which pass their gametophytic and sporophytic stages upon wholly unlike and unrelated hosts. It was natural, therefore, to direct chief attention, especially at first, toward unraveling the tangle of heteroecious forms.

Nobody knew how many rusts were to be found on the North American continent and its islands. There were possibly a thousand or more names in existence, but how many of these names applied to single and independent life cycles, and how many to parts of cycles, or were synonyms, no one had attempted to say. It was, in fact, only with the existing names that I had to do. It was no part of my problem to discover new species, or to give new names, either in preparing manuscript for the North American Flora, or in conducting cultures, except in so far as these were required for the systematic development of the work. Many longer or shorter excursions were made during the progress of the cultures, some of them a thousand miles or more, but they were all for the purpose of making field observations upon known species, and in no case for making discovery of new species. The new species that were found were an incidental result.

The first year of the culture work, that of 1899, was very encouraging, and developed no particular difficulties calling for solution. So far custom was followed in the application of names, and it had not been necessary to apply any formula to decide what constituted a species. The assumption that forms on the same or closely related hosts, having no striking morphological differences, were of one species seemed a sufficient hypothesis, and the corollary necessarily followed that cultures would show the range of hosts for each species, as well as serve to demonstrate the stages and spore-forms in the life cycle. Certain features in connection with the common Euphorbia rust did indicate that difficulty might be found in the application of the

corollary, and this indication became more pronounced during the year following.

In 1902 three species of Euphorbia of unlike appearance and growth habits were found to bear non-interchangeable rusts, which were tentatively considered to present races of *Uromyces Euphorbiae* C. & P., and with the more confidence because no well-defined morphological distinctions could be detected. Subsequent studies strengthened this view of races, and the idea of races from this time on was constantly kept prominently in mind. The attempt to evade or simplify taxonomic and cultural difficulties by treating such races or biological strains as species, as Tranzschel[2] subsequently did with these same Euphobia forms was not favored.

It was also in 1902 that the Helianthus rust was grown with indication of races, developed further in the following year, and brought to a climax in 1904, with the conclusion that a number of more or less well established races occur in *Puccinia Helianthi* Schw., having *Helianthus annuus* as a bridging species, following the lead of Marshall Ward[3] in his study of the brome rusts. No further considerable effort was made to study races in autoecious species, or to pick out bridging hosts, as it was held that to ascertain the identity of species was as great a task as could be undertaken in this series of cultures, and that studies leading to the separation of a species into varieties, races, forms, or other subclasses, although of much biological and often of great economical interest, must be left for other time and hands.

The problems of the Carex rusts came early into view. In 1901 and 1902 the three remarkable co-species, having telia on various species of Carex and aecia on species of Aster, Solidago and Erigeron respectively were repeatedly grown from telial material, and were called *Puccinia Caricis-Asteris, P. Caricis-Solidaginis,* and *P. Caricis-Erigerontis.* As no single collection of teliospores was found that would infect more than one of the genera named, the forms were tentatively considered to be species and given distinctive names, followng the brilliant cultural methods of Klebahn in Germany, Plowright in England, and

[2] Ann. Myc. 8: 1–35. 1910.
[3] Ann. Myc. 1: 150. 1903.

others, although a careful comparison of the three forms made it seem "not improbable that the three represent more correctly the biological variations of one species," as was stated at the time. In the further study of these forms it was thought that the telial stage might be found to be restricted to certain species of Carex, or to particular sections of the genus, as was believed to be true of the European Carex rusts, which assumption in the case of the American forms, however, could not be established in any definite way. The hosts were shown finally to be even less restricted than supposed, as the Aster form was eventually carried over to Euthamia for its aecia and to Dulichium for its telia.

The necessity soon became acute to find criteria by which to judge of the standing of species among the rusts, and all the more so because the manuscript was now under preparation for the North American Flora. It was soon decided that, for the purposes of the Flora, morphological characters must be the final test for species. Yet for purposes of study outside of taxonomy it might be serviceable and desirable to maintain the so-called biological or physiological species in any rank desired, but they ought not to be recognized as species proper in taxonomic classification. Consequently in 1912 the three Carex forms were combined with certain European forms under the name *Puccinia extensicola* Plowr., a name which has been supplanted by *P. Asterum* (Schw.) Kern, since the cultural series closed. Furthermore, the cultures of 1913 disclosed that *P. vulpinoidis* with its covered telia had its aecia on Solidago, and was a part of this same species heretofore known only with naked sori, making the much emphasized character of covered telia a secondary one to be associated principally with the host.

Thus the idea of species among the rusts grew into a far more definite, although more complex form, than could have been possible without the aid of cultural studies. A liberal view was now also required regarding hosts, and also the stress on certain morphological characters called for modification, but the end was not yet.

In 1910 a number of cultures with the Carex rust, *Uromyces perigynius,* revealed a remarkable parallelism between this species

and *Puccinia extensicola.* Aster and Solidago races came to light, not however quite so well stabilized in some instances as with the corresponding Puccinia races, for in one case sowings of teliospores from the same Carex collection were made to grow on both Aster and Solidago. The two species, one of Uromyces, the other of Puccinia, were subjected to an extensive microscopical study, and no marked differences could be found between their several corresponding spore-forms, except in the septation of the teliospores. This unity of structure had already been observed regarding the aecia and aeciospores when a preliminary culture of the Uromyces was made seven years before. From the microscopical evidence, united with much collateral evidence, the following statement was made in the discussion of 1910, which holds true to the present time: "As the aecia and uredinia of the two groups [of host-races], one under the genus Puccinia and the other under Uromyces, are indistinguishable, and as the teliospores of the Uromyces agree with the one-celled spores of the Puccinia [mesospores] and also with the two-celled spores in all characters except number of cells and consequent length of spore, the former doubtless are morphological races of the latter. Relationship could be shown better by putting all of these forms under one specific name, and designating the several races by varietal names. But in the present state of taxonomy of the rusts it is more convenient to dispose of them under the two genera: *Puccinia* and *Uromyces.*"[4]

If any further illustration were needed to show that Puccinia and Uromyces were not only parallel genera but actually identical, it was supplied by the cultures of the following year, 1911. During this season successful cultures on *Atriplex hastata* of both *Uromyces Peckianus* and *Puccinia subnitens,* each grown from teliospores on the grass, *Distichlis spicata,* obtained from widely separated localities, gave rise to aecia that appeared to be indistinguishable. A morphological study of these two so-called species has been reported by C. R. Orton in his article on "Correlation between Puccinia and Uromyces,"[5] in which he finds a

[4] Mycologia 4: 22. 1912.

[5] Mycologia 4: 199. 1912.

slight difference in size of the urdiniospores, and, of course, in the teliospores a difference in number of cells and consequent size. He points out, however, that these differences are such as are to be expected in other similar cases. The comparison of these two forms of Distichlis rust, as to morphology, hosts and distribution, is an interesting topic, which need not be pursued further here.

If the Carex-Aster-Solidago-Erigeron studies supplemented by studies with the Distichlis rust, opened up new views of the species question in relation to host influence and teliosporic dimorphism, so did the Carex-Ribes studies disclose new views in another direction. The first cultures were in 1901. As the results of sowing teliospores on Ribes gave peculiarly small and pale aecia, it was thought that an unrecognized species had been found, which was called *Puccinia albiperidia.* Whether this form was distinct from the common Carex-Ribes rust of the fields, distinguished as *P. Grossulariae,* and whether American forms were distinct from European forms, of which Klebahn had recognized five, were questions which received attention from year to year as opportunity permitted. In this study Dr. Klebahn graciously consented to lend assistance, and during the two seasons of 1904 and 1906 made cultures at Hamburg, Germany, from telial material supplied by the writer.

Just as the problem seemed solved, and Dr. Klebahn[6] and myself had independently arrived at the conclusion that in both Europe and America only one heteroecious species occurred, which possessed a number of strains or races, it was discovered by C. R. Orton,[7] while assisting with the rust studies, that the original material of *P. albiperidia* on*Carex pubescens,* as well as that on a number of American species of Carex similar to *C. gracillima,* possessed urediniospores with only one basal pore, in part at least, instead of the usual three or four equatorial pores. Again the Carex-Ribes rusts of Amercia seemed to fall into two species, not based on differences in the aecia this time, but on differences in the urediniospores. From 1910 onward the question in this connection was whether or not the same species of rust

[6] Zeits. Pflanzenkr. 17: 132–134. 1907.

[7] Mycologia 4: 14, 200. 1912.

could possess urediniospores partly with one basal pore and partly with three or four equatorial pores. The answer involved the value and application of pore characters in defining species. After special search,[8] which led to both kinds of urediniospores being found repeatedly in the same sorus, although for the most part they occurred in separate sori, it was concluded that only one species of rust was under consideration, but with morphological as well as physiological races, not well delimited.

It seemed probable, furthermore, that the previously described, one-pored form of Carex rust, known as *Uromyces uniporulus* Kern, was a race also belonging to the Carex-Ribes species, but it was not possible to test the matter by cultures. In this connection it is interesting to note, and provocative of speculation, that there is no form yet known with three- and four-pored urediniospores belonging under Uromyces in the Carex-Ribes aggregation, to make the parallelism with its Puccinia form complete.

In 1917, the last year of the culture series, the principle of basing species upon morphological characters, with a greater or less degree of mobility in interpretation, was further illustrated by the case of the Spartina rust, *Uromyces Polemonii* (Peck) Barth., which it was found could be segregated into four races,[9] separable by small but appreciable differences in morphological characters of both aeciospores and teliospores, and by wholly unrelated aecial hosts, and further reinforced by some differences in habitat and geographical distribution. The correlated Puccinia-form for this common and widely distributed American rust is that of *Puccinia Distichlidis,* so-called because the type collection was incorrectly labelled as on Distichlis instead of on Spartina. Its range and aecial hosts, so far as known correspond to only one of the four Uromyces races.

At the time the culture work began the subepidermal rusts occurring on wild grasses in America with few exceptions, passed under the name of *Puccinia rubigo-vera,* along with part of the similar leaf rusts of cereals. No criteria had been found for distinguishing them, not even those which had received special

[8] Mycologia 7: 67–69. 1915.
[9] Mycologia 9: 309–312. 1917.

names, and every effort was consequently put forth to make headway into this obscure maze of forms. The first success was in 1902 with a form on *Elymus virginicus* and aecia on Impatiens, which became *Puccinia Impatientis* (Schw.) Arth. The work opened up slowly. In 1903 a false move was made in connection with the rust on Bromus, but the year following this rust was shown to have aecia on *Clematis virginiana*.[10]

In 1907 *Puccinia Agropyri* E. & E., as it occurred in Colorado on Agropyron, was found to go to *Clematis ligusticifolia*, a connection that had been demonstrated by Dietel with European hosts fifteen years before. The following year *Puccinia cinerea* Arth. on Puccinellia was grown on *Ranunculus Cymbalaria*, a rust from *Koeleria cristata* on Mahonia, from Bromus on Thalictrum, from Agropyron on Aquilegia, the last three being described as new species. In 1915 aecia on Hydrophyllum from Utah were made to grow on Agropyron and Elymus, giving rise to uredinia and telia similar to those from the Ranunculaceous aecia, but believed to constitute a distinct species. In 1916 another rust on *Koeleria cristata* was grown on Laciniaria under the name *P. Liatridis* (Ell. & And.) Bethel. Repeated attempts were made to find the aecial host of the common leaf rust of wheat, *P. triticina* Erikss., but without success, although there were many indications that pointed to a Ranunculaceous host, and especially to Clematis or Anemone. It was thought that a favorable trial on *Clematis Flammula* would give a measure of success. At any rate it was believed to be one of the numerous races of the subepidermal leaf-rust of grasses, *P. Agropyri*, with Ranunculaceous hosts for its aecia.[11]

The series were discontinued before the study of the subepidermal forms was completed, but ten of them had been connected with their aecia. The conviction had been growing for some time that some of these ten names represented races of *Puccinia Agropyri*, rather than independent species, as was stated in discussing the cultures of 1912. When the manuscript was pre-

[10] For a full account and explanation of the mistake of 1903 in supposedly connecting aecia on Dirca with the Bromus rust see Journal of Mycology 11: 62–63. 1905.

[11] Mycologia 9: 276. 1917.

pared for the North American Flora *P. tomipara, P. Agropyri, P. cinerea, P. alternans* and *P. obliterata,* as well as *P. triticina,* were placed under the one name of *P. Clematidis* (DC.) Lagerh. It is considered a great advance to bring from the limbo of *P. rubigovera,* six distinguishable species, some of them having a considerable number of recognized races, and thereby making it possible to relegate to obscurity some dozen or more names that had previously been encumbering the literature of the rusts.

In a somewhat similar way the American Carex rusts were in utter confusion at the beginning of the cultures. They were quite generally called *Puccinia Caricis* or *P. caricina,* no cultures with American material having been made, and diagnostic characters not having been well worked out. Altogether ten species were grown during the culture period to show their full life cycle, and in several of them a number of races was found, including the one-celled *Uromyces perigynius.* Of course, being able to separate these ten species made it possible to decide upon the identity of other species, which were not actually grown.

A view generally held when the culture work began was that the hosts of an autoecious species, or of each of the two parts of a heteroecious species, would be found to be closely related, often, indeed, to be but a single species, or genus, and certainly always within a single family. Consequently it was felt that when a grass or sedge rust was successfully cultured, the problem about hosts for that species was practically solved. This complacent opinion was quite upset in the case of *Puccinia subnitens* Diet. on *Distichlis spicata,* which in 1902 was first grown upon *Chenopodium album.* In 1904 Rev. J. M. Bates of Nebraska, who had made the field observations and suggestions for this combination, wrote that he had been continuing his observations of this species and believed that it had aecia also on hosts belonging to two other families, which seemed to the writer at the time as most incredible. Tests, however, showed it would flourish on species of Cleome, Lepidium, Sophia and Erysimum, as well as on Chenopodium, compelling the admission that it would grow "with equal vigor upon species belonging to three families of plants," at the time being a "remarkable fact not known for any

other species of rust." Additional genera in the same families were added from time to time for aecial hosts, until in the cultures of 1916 the species was grown on Abronia and Polygonum, thus adding two more families. Mr. E. Bethel, of Denver, Colorado, who made the field observations and suggestions for the later additions, has continued the list since the culture series stopped and brought the number up to 76 species, belonging to 19 families,[12] a truly astonishing showing, and all the more so as no clearly defined races have so far been detected. The only other species of rust with such a remarkably extended series of aecial hosts at all approaching *P. subnitens* Diet., is that of *P. Isiacae* (Thüm.) Wint.. from the dry trans-Caspian region of western Asia, as reported by Tranzschel.[13] This species with telia on *Phragmites communis* has aecia on 19 species of hosts belonging to 9 families, the aecial families being the same as for *P. subnitens.*

In still another way the conception of species was modified when in 1905 teliospores from *Ruellia ciliosa* were grown on the same host and also on *R. strepens.* The latter host, with loose, watery tissues, gave rise to aecia fully ten per cent. larger in every way than did the former host with its firm, woody tissues, thus showing that the forms recognized by the Sydows under *Puccinia lateripes* B. & Rav. and *P. Ruelliae* (B. & Br.) Lagerh.[14] represent only a host influence upon one and the same species, this influence being traced not only in the aecia, but also in the other spore-forms.

Thus it will be seen that while the main work of the cultures was effective in completing the life cycles for many species, and in some cases extending and defining the range of hosts, it was at the same time most profoundly modifying the current conception of species among the rusts. Instead of a rigid ideal of a few invariable characters and a limited range of nearly related hosts to be determined by cultures, we have substituted a complex of somewhat variable morphological characters as the basis,

[12] Bethel, Phytopathology 9: 193. 1919.

[13] Beiträge zur Biologie der Uredineen. Trav. Mus. Bot. Acad. Sci. St. Petersb. 3: 40. 1906; 7: 14. 1909.

[14] Sydow, Monographia Uredinearum 1: 235. 1902.

with a more or less extended range of hosts in part determined by cultures and in part by microscopical similarities in the fungus. A species at the beginning of the work was conceived as a simple and direct succession of individuals of the same appearance, capable of being demonstrated by cultures, but at the close had become a bundle of somewhat mobile characters, often comprising many strains varying physiologically and sometimes morphologically, and to a more or less extent not interchangeable by cultures.

In some other ways than already mentioned the accepted notions regarding rusts were modified. It was found that teliospores among the grass forms were not all necessarily resting spores, and that the non-resting forms presented special problems, whose solution was not far advanced when the work came to a close. Assistance with field observations and material permitted successful cultures to be made in May, 1911, with the aeciospores from Arabis sown on Trisetum. The Arabis aecia arise from systemic mycelium extending throughout the stem and leaves of the plant. A month later teliospores resulting from this culture, now having become mature, were found to be capable of germination and were sown on seedling rosettes of Arabis. The results of this sowing first definitely showed when the axis of the Arabis began to elongate as growth started the following spring. A culture was similarly carried out in 1903 with *Puccinia Eatoniae,* using the aecia on *Ranunculus abortivus,* also a form with diffused mycelium, but a reciprocal culture was not made. These two species of rusts, having a systemic form of aecia, were the only ones of the kind which were brought under culture. They belong to an interesting class physiologically, with systemic aecia, and with teliospores capable of germination upon maturity, which possibly do not retain their viability through the winter, or only to an impaired degree.

The culture work began with the too prevalent idea that all rusts could be expected to conform in general to the well known *Puccinia graminis.* It closed with the conviction that the rusts are far too diversified in their morphology, their numerous characters, their physiological adaptations, and their range of hosts,

to be represented by *Puccinia graminis* in more than one out of numerous aspects. In this resumé of cultures only a few of the more prominent developments that should help to modify the too rigid and restricted ideas of rust species as commonly held have been brought forward. Yet enough has been said possibly to indicate the value of what has been accomplished and the need of more extended work along similar lines.

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